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On the Miocene Bug Genus *Diacorixa*, with the Description of a New Fossil Species from Southern Germany (Insecta: Heteroptera, Corixidae)

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With 14 figures

Summary

The first fossil bugs from Miocene sediments (Sarmatian) of the Randeck Maar, Southwestern Germany (Swabian Alb), are dealt with. The following families are recorded: Corixidae (*Diacorixa germanica* n. sp.), Notonectidae (*Anisops* sp. prope *deichmuelleri* Schlechtendal 1894), Saldidae (*Oligosaldina* sp.), Cydnidae and Pentatomidae. The water boatman *Diacorixa germanica* n. sp. belonging to the recent subfamily Corixinae (tribe Corixini) from the Randeck Maar (collection of the Natural History Museum Stuttgart) is described. *Diacorixa miocaenica* Yu. Popov 1971 is redescribed from the holotype and paratypes from the Miocene of North Kirghizia (USSR).

The Corixinae are derived from the Diapherininae due to the Cretaceous genus *Diapherinus* Yu. Popov 1966 being treated as the direct ancestor of *Diacorixa*. Evolution of hemelytral structures, the suprageneric classification of Corixinae and phylogenetic interrelations of Corixidae are discussed. A new phylogenetic scheme of corixid subfamilies is given.

Zusammenfassung

Erstmals werden fossile Wanzen aus Sedimenten des Randecker Maars (Miozän, Sarmat) in Südwest-Deutschland (Schwäbische Alb) beschrieben. Folgende Familien wurden nachgewiesen: Corixidae (*Diacorixa germanica* n. sp.), Notonectidae (*Anisops* sp. prope *deichmuelleri* Schlechtendal 1894), Saldidae (*Oligosaldina* sp.), Cydnidae und Pentatomidae. Die Ruderwanze *Diacorixa germanica* n. sp. (Unterfamilie Corixinae, Tribus Corixini) wird vorgestellt. *Diacorixa miocaenica* Yu. Popov 1971 wird anhand von Holotypus und Paratypen aus dem Miozän von Nord-Kirgisien (USSR) erneut beschrieben.

Die rezente Unterfamilie Corixinae läßt sich von der fossilen Unterfamilie Diapherininae über die kretazische Gattung *Diapherinus* und die miozäne Gattung *Diacorixa* ableiten. Die Evolution der Strukturen der Vorderflügel, die Klassifikation der Corixinae im Tribus-Niveau sowie die verwandtschaftlichen Beziehungen innerhalb der Unterfamilien der Corixidae werden diskutiert. Ein neues phylogenetisches Schema der Unterfamilien der Corixidae wird gegeben.

1. Introduction

During my research trip to West Germany in 1982, I was privileged to examine over 100 fossil bugs from the Miocene deposits of the Randeck Maar, Swabian Alb, kept in the collection of the Staatliches Museum für Naturkunde in Stuttgart

(SMNS), as well as one further imprint from the Upper Miocene deposits of the crater Lake Nördlinger Ries near Wemding, Southern Germany, from the collection of the Bayerische Staatssammlung für Paläontologie und historische Geologie in München (BSPG). No bugs from either deposit have been hitherto reported, though insect remains are known to be very rich and diverse. Thus, the SMNS collection from the Randeck Maar is wealthy in Isoptera (ARMBRUSTER 1938, 1941a), Hymenoptera (ARMBRUSTER 1941b), Lepidoptera (REISS 1936), Coleoptera (SCHAWALLER 1986), whereas that from the Nördlinger Ries (over 2000 remains) is still completely unknown (BOLTEN et al. 1976).

The present paper puts on record the first fossil bugs from both localities and the following families. The Corixidae are dominant, with the single species *Diacorixa germanica* n. sp. involved. Among the other water bugs, the Notonectidae are represented by *Anisops* sp. prope *deichmuelleri* SCHLECHTENDAL 1894 also known from the Upper Oligocene of Rott, Northwest Germany (STATZ 1950, POPOV 1971, ŠTYS & ŘIHA 1975). Shore bugs include Saldidae (*Oligosaldina* sp.) somewhat resembling *Oligosaldina* spp. from the Upper Oligocene deposits of Rott; those species described in STATZ & WAGNER (1950) are now soundly suspected to have been in fact one single form (COBBEN 1980). A few terrestrial bug remains belong to both Cydnidae and Pentatomidae (?Phyllocephalinae). Some of the above fossils are treated below, some are planned to be treated later as a separate paper.

Taking the opportunity to describe another *Diacorixa* YU. POPOV 1971 as based on a better preserved and not less rich material, I have ventured here a revision of the generotype *D. miocaenica* YU. POPOV 1971 from both holo- and paratypes deriving from the Miocene Lake Tchon-Tuz in Kirghizia, Tien-Shan Mts., USSR, and kept at the Paleontological Institute of the USSR Academy of Sciences, Moscow (PIN). As a result, some new important characters have been revealed warranting a redescription of both genus and genotype to be provided herein.

Acknowledgements

I wish to extend my deep gratitude to Dr. M. Warth, Stuttgart (SMNS), for the help and encouragement I experienced during my short stay in Stuttgart, and to Dr. R. Förster, Munich (BSPG), for the opportunity to study certain fossil bugs during my short visit to Munich. Besides, Dr. S. Golovatch, Moscow, kindly checked the English of the final draft. I am also indebted to Dr. W. Schawaller, Stuttgart, for the help in publishing this paper.

2. Geological background

The age of both Randeck Maar and Wemding (Early Sarmatian) is estimated as 14.6 ± 0.6 mil. years (BALLMANN 1983, GREGOR 1986). The age of the Tchon-Tuz deposit is less strictly known and now considered as Lower–Middle Miocene (TARASOV 1970).

The Randeck Maar deposit was formed inside a volcanic crater embodying a freshwater lake. On the other hand, the Tchon-Tuz locality was a large, shallow, brackish water body. Interestingly, the lake deposits of Randeck Maar contain a subequal proportion of imagines and nymphal instars of *Diacorixa germanica* n. sp., whereas no nymphs of *D. miocaenica* YU. POPOV 1971 are known from the Tchon-Tuz over a similar background of numerous imprints involved.

3. Systematic part

Suborder Heteroptera
Infraorder Nepomorpha Yu. Popov, 1968
Family Corixidae Leach, 1815
Subfamily Corixinae Leach, 1815
Tribe Corixini Leach, 1815

Genus *Diacorixa* Yu. Popov, 1971

1971 *Diacorixa* Yu. Popov, p. 137.

Type species: *Diacorixa miocaenica* Yu. Popov 1971 from the Miocene of North Kirghizia, USSR.

Diagnosis. – Small-sized, less than 6 mm long. Body oblong-oval, ca. 2.5 times longer than wide. Eyes not protuberant; postocular space very narrow. Pronotum light brown, rather transverse, with a short longitudinal carina at front margin. Hemelytra smooth, subtransparent, corium and clavus with dark narrow clear stripes along outer and inner sides and at border between corium and membrane, stripe of inner side of corium passing onto base of membrane; white frosted (pruinose) areas*) (clavopruina, prenodal and postnodal pruinoses) well-developed; coriopruina absent, clavopruina large, slightly shorter than postnodal pruina and more than 1.5 times as long as dark inner stripe along Pcu, postnodal pruina less than 1.5 times as long as prenodal pruina; embolium rather flattened; the shiny prenodal area of costal margin very short; costal fracture oblique; border between corium and membrane hardly distinguished. Abdominal tergum VI of males apparently without strigil (file-like plate); abdominal asymmetry feebly dextral.

Species. – Besides the type species *D. miocaenica*, this genus comprises only one species, *D. germanica* n. sp. from the Miocene of the Randeck Maar and Wemding in Southern Germany (BRD).

Comparison. – The genus *Diacorixa* differs well from all genera of Corixinae by the rather flattened costal margin (especially embolium) and clavopruinose area of the hemelytra. Presence of dark stripes on the hemelytra and undeveloped coriopruina distinguishes this genus from all genera of the tribe Corixini. The nympha also has very specific features such as the short metanotum and the hairy meso- and metanotum.

Diacorixa miocaenica Yu. Popov
Figs. 1, 13, 14

1971 *Diacorixa miocaenica* Yu. Popov, pp. 137–138, fig. 89, pl. 6, fig. 3, 4.

Holotype: Imago from Miocene sediments of Tchon-Tuz locality, North Kirghizia, Kotchkorskaya despression, right bank of Tchon-Tuz river; deposited in the collection of the USSR Academy of Sciences, PIN no. 372/16 (Fig. 1, 13, 14).

Paratypes: Imago PIN no. 372/1–3, 16–19, 25–27, 30, 32, 33, 50, 51, 64, 68, 72, 73, 96, 101, 102, 114, 144, 166, 171, 484, 486, 488, 508, 509, 517, 519, 520, 530, 533, 535, 634, 639–642, 647–650, 652, 656–658, 660, 662–665, 671–674, 684, 686, 687, 692, 693, 699, 701–709, 713–716 from the same locality.

*) The term ‚white frosted areas' is used after Lauck (1979) and Jansson (1986).

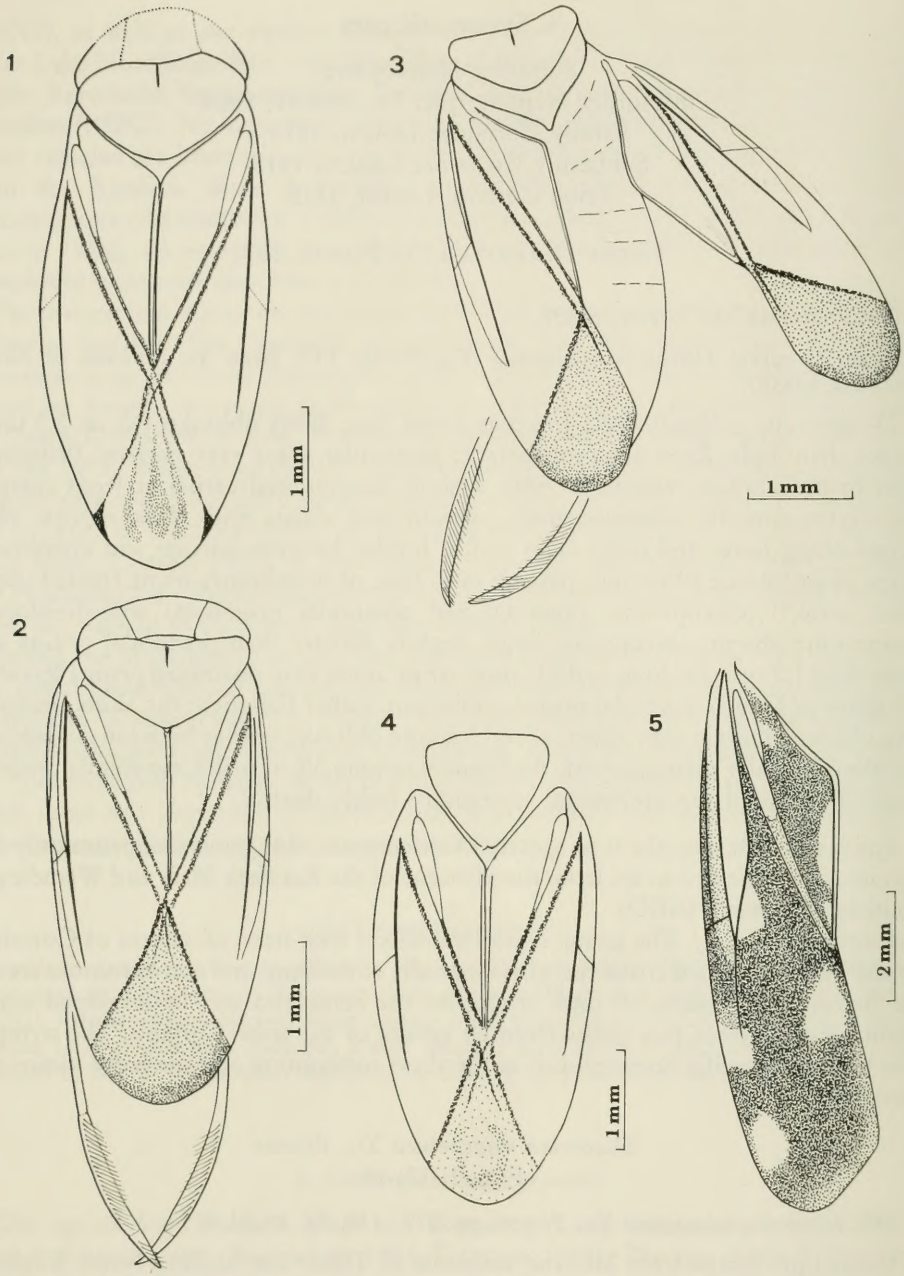

Fig. 1. *Diacorixa miocaenica* Yu. Popov, Holotype, PIN no. 372/16, Tchon-Tuz, North Kirghizia, USSR.

Fig. 2–4. *Diacorixa germanica* n. sp.
2: Holotype, Inv.-Nr. 26498, Randeck Maar, Southwest Germany.
3: Paratype, Inv.-Nr. 26501, Randeck Maar, Southwest Germany.
4: Paratype, Inv.-Nr. 1966 XLII 15, Wemding, Southern Germany.

Fig. 5. *Diapherinus ornatipennis* Yu. Popov. Holotype, PIN no. 1989/3438, Baissa, Transbaikalia, USSR.

Imago. – Body dark brown, pronotum and hemelytra finely punctate; inner angle of membrane at apex of corium narrowly dark and membrane with three longitudinal darkish stripes. Pronotum 1.6 times broader than long, lateral angles and apex widely rounded. Hemelytra dorsally slightly convex, ratio of prenodal and postnodal pruinose areas as 1.2:1, dark inner stripe of clavus and clavopruina as 1.5:1, postnodal pruina and clavopruina as 1.2:1.

Size. – Length from apices of hemelytra 5.0–5.8 mm, length of hemelytra 4.2–4.4 mm, width 2.1–2.3 mm.

Diacorixa germanica n. sp.
Figs. 2–4, 7-11

Holotype: Imago from Miocene sediments of the Randeck Maar in Southern Germany (Swabian Alb), deposited in the collection of the SMNS, Inv.-Nr. 26498.

Paratypes: Imago Inv.-Nr. 26489, 26491–26495, 26498, 26500–26503, 26506, 26509 (+nympha), 26511, 26512, 26520, 26522–26525, 26529, 26531, 26532, 26536–26538, 26542 and more than 20 specimens, not marked, from the same locality and deposited in the SMNS; one specimen from Wemding (Nördlinger Ries, Bayern), deposited in the collection of the BSPG (München), Inv.-Nr. 1966 XLII 15 (Fig. 4); nympha Inv.-Nr. 26499, 26508, 26526–26528, 26534, 26535, 26539, 26540, 26543, and more than 40 specimens, not marked, from the same locality. Two specimens (imago) and one nympha were donated by SMNS to the collection of the PIN USSR, PIN no. 4391/1–3.

Imago: Body dark brown, pronotum and hemelytra finely punctate, outer margin of membrane narrowly darkish. Pronotum 1.8–1.9 times broader than long, lateral angles and apex widely rounded. Hemelytra dorsally slightly convex, ratio of prenodal and postnodal pruinose areas as 1.3:1, dark inner stripe of clavus and clavopruina as 1.2:1, postnodal pruina and clavopruina as 1.1:1.

Size: Length from apices of hemelytra 4.2–4.9, length of hemelytra 3.8–4.1, width 2.0–2.1.

Nympha (last instar) (Fig. 11): Body ca. 4.0 mm, oblong-oval, twice as long as wide. Head transverse, 2.3 times longer than wide. Metanotum medially shorter than mesonotum; long hairs covering entire hind margin of wing-pads, mesonotum and metanotum, disc of mesonotum and metanotum with long hairs. Abdomen nearly bare; dorsal abdominal pattern quite distinct, apertures of all scent-glands relatively large.

Comparison. – Differs from *D. miocaenica* by the more transverse pronotum, ratio of pruinose areas of the hemelytra, colour of the membrane and smaller size.

4. Discussion

Unfortunately, the morphology of Corixidae has never been treated monographically, and separate details of external structure are dealt with in various papers. On the other hand, paleontological material fails to preserve certain important characters necessary for phylogenetic reconstructions. Only a number of external features of the body are preserved, in particular those of the hemelytra, which are considered and discussed below in further detail in connection with certain problems of corixid classification.

The main trends in the adaptive evolution of the Corixidae seem to have been the formation of certain head structures (due to the development of phytophagy, i. e. algo- and detritophagy, alongside with predation), thorax (pronotum completely

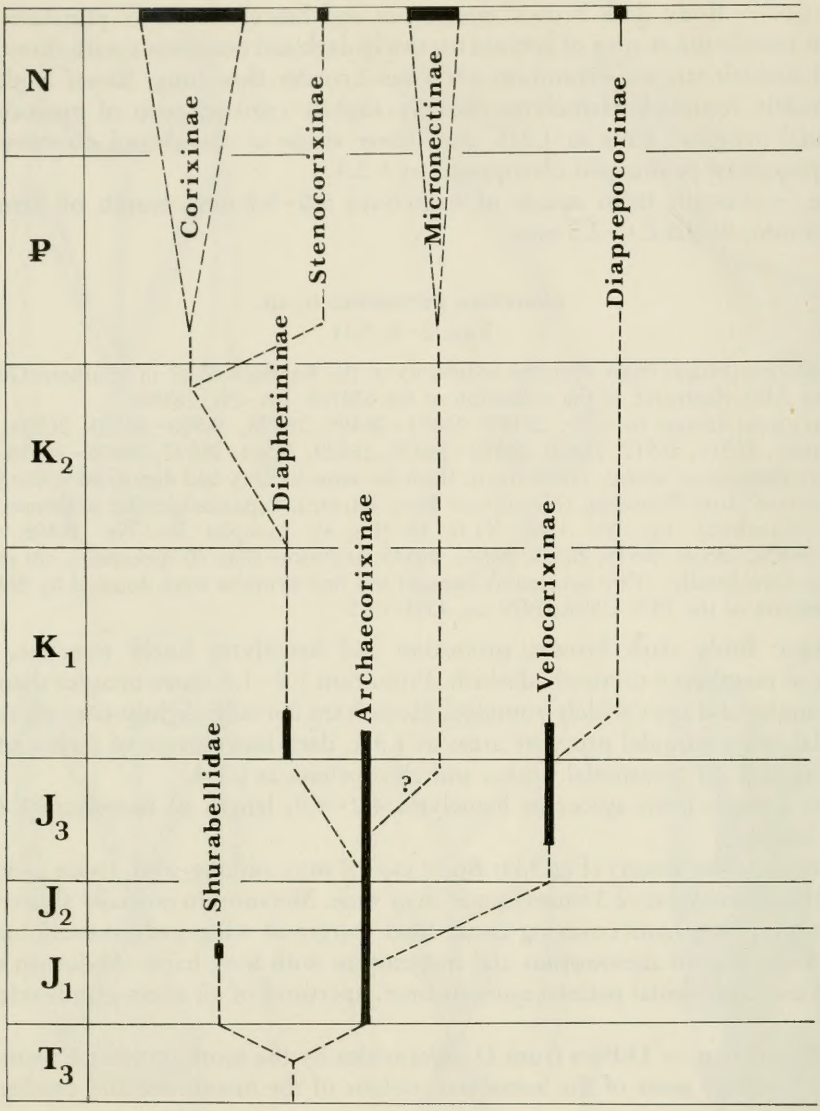

Fig. 6. Phylogenetic scheme of interrelationships of both fossil and recent subfamilies of the Corixidae.

covering the scutellum; pleural areas), hemelytra (emboliar groove; white frosted areas), legs (palae of the fore legs; fore femoral peg fields; flattened hind legs), and strigil (a file-like plate on the ♂ tergum VI).

The evolution of hemelytral morphology within the subfamily Corixinae seems to have been directed to the formation of a relatively broad emboliar groove and white frosted areas (pruina), as well as to the development of both texture (smooth, rugose, rastrate) and pattern (transverse dark stripes or netting). The structure of the hemelytra in the Miocene *Diacorixa*, in particular both embolium (i. e. prenodal area) and clavopruinose area flattened, allows to elucidate direct ancestry from that of the

Early Cretaceous Diapherininae from East Asia (Transbaikalia, Mongolia, China). Besides, the Mesozoic *Diapherinus* Yu. Popov 1966 had already a complete set of well-developed pruinose areas in which the costal fracture was connected with R in front of al long prenodal pruina (an apomorphy), whereas the postnodal area had not yet been transformed into a pruina (a plesiomorphy). A very short postnodal pruina is also observed in a good number of corixine genera such as *Corixa* Geoffroy 1762, *Trichocorixa* Kirkaldy 1908, *Arctocorisa* Wallengren 1894, *Callicorixa* White 1873, *Sigara* Fabricius 1775 *(Lasiosigara* Hungerford 1948, *Phaeosigara* Hungerford 1948, some species of *Vermicorixa* Walton 1940). This pruina is especially short in *Centrocorisa* Lundblad 1928 and *Morphocorixa* Jaczewski 1931, in which the postnodal/prenodal length ratio is 1:2.5. Judging from all the Corixidae known at the present, both recent and fossil, they are the postnodal area, coreopruina, clavopruina, and hemelytral coloration that are subject to transformation. The hemelytral structure of the Early Cretaceous Diapherininae shows that the evolvement of white frosted areas was apparently heterochronous. At least as regards the postnodal pruina, it seems to have been formed the latest, and its underdevelopment in some recent Corixinae (e. g. *Agraptocorixa)* could obviously reflect a plesiomorphy. A shiny precostal area of the costal margin, when present, is very short in Corixidae. Some recent genera of Corixinae have a shiny precostal area very variable in length, but never longer than a half of the embolium. On the other hand, the shiny postnodal area in *Diapherinus ornatipennis* Yu. Popov 1966 is very long and narrow, almost as long as the embolium.

The transformation of hemelytral structures in Micronectinae seems to have been directed to the development and conservation of a very narrow and flattened emboliar groove with a very short costal fracture, but without white frosted areas so characteristic of both Corixinae and Diapherininae. The least modified hemelytral structures might have been retained in the primitive Diaprepocorinae as well as the closely related Jurassic Archaecorixinae, both characterized by such symplesiomorphies as the somewhat flattened costal margin, short and broad clavus with an arched Pcu, complete absence of white frosted areas and depigmentation.

The position (either direct or oblique) and state of development of the costal fracture is also subject to variation in the Corixinae. Normally, the costal fracture crosses the entire pruinose area to join the apex of R, whereas the medial fracture does not reach to the costal one. However, in *Hesperocorixa distanti* Kirkaldy 1908, R crosses the costal fracture as a trachea; in *Cymatia* Flor 1860, the costal fracture turns gradually into the medial one, failing to reach to the emboliar groove's inner margin, contrary to the erroneous observation by Jansson (1986) as if the Cymatiainae lack a costal fracture (= nodal furrow).

The depigmented dorsum in a number of species belonging to recent genera of Corixinae may be suggested as being a plesiomorphy. Pigmentation in the course of corixine evolution seems to have affected first the pronotum *(Ramphocorixa* Abbott 1912, in which it is hardly traceable), later the clavus (*Morphocorixa* Jaczewski 1931) and finally the remaining parts of the hemelytra in the form of transverse bands or netting (the majority of the Corixinae). In the aberrant genus *Agraptocorixa* Kirkaldy 1898, both pronotum and hemelytra are completely depigmented, the latter being translucent. In the recent primitive Diaprepocorinae, no pattern is likewise observed. The majority of the known Mesozoic Corixidae and Shurabellidae were

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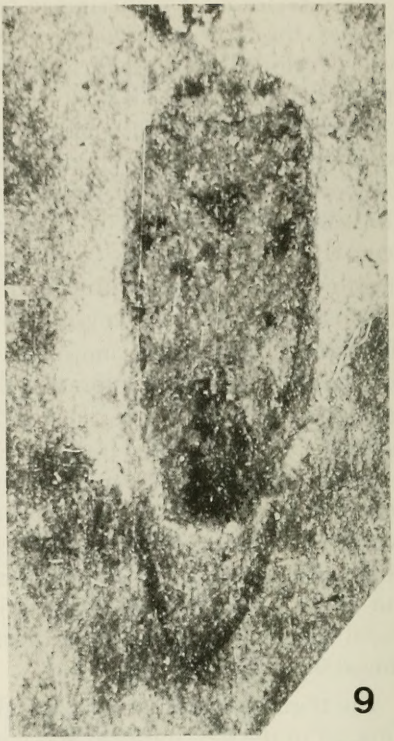
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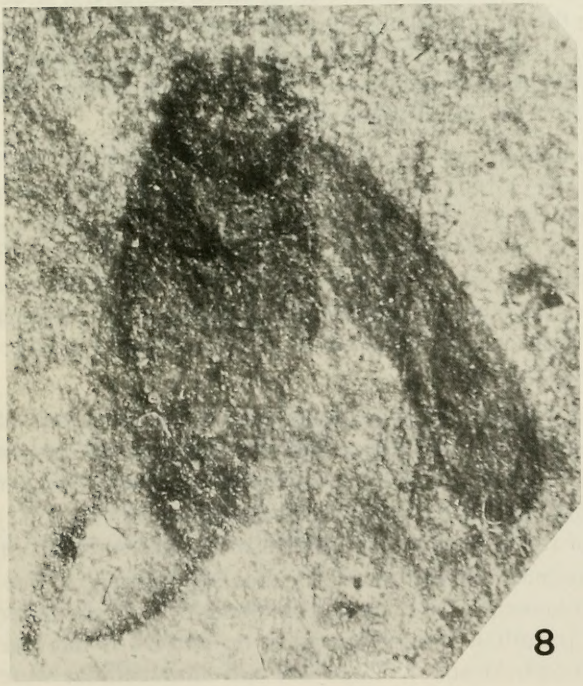
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also depigmented, except for the spotted Early Cretaceous Diapherininae (Fig. 5, 12).

The conspicuous stripes along the inner and outer margins of both corium and clavus in the Miocene *Diacorixa* were also present in the Early Jurassic micronectines *Dichaspis laesa* BODE 1953 (= *Strobilocoris mediocordatus* BODE 1953) and *Acromocoris angustus* BODE 1953 from the Upper Lias (Lower Toarcian) of Lower Saxony. Both have erroneously been placed by BODE (1953) within the lygaeoid family Pachymeridiidae (= Sisyrocoridae), but actually represent Corixidae and possibly even one single species.

Finally, the development of the hind margin of the pronotum completely covering the scutellum, retention of 4-segmented antennae and evolvement of abdominal asymmetry due to the strigil on the ♂ tergum VI are characteristic of the corixid lineage encompassing the Diapherininae, Corixinae and Stenocorixinae. However, the Diapherininae had yet not reached the evolutionary stage implying the apparition of both strigil and abdominal asymmetry. In fossil Corixidae a strigil was definitely present in *Corixa rhenana* STATZ 1950 from the Upper Oligocene of Rott, North-West Germany (s. STATZ 1950).

The recent aberrant Stenocorixinae display a feeble abdominal asymmetry in the males combined with the absence of a strigil. Similarly, in a number of recent corixine genera a strigil is also wanting (e. g. *Callicorixa* WHITE 1873, *Paracorixa* POISSON 1957, *Morphocorixa compacta* HUNGERFORD 1948). Still the relationship between the Stenocorixinae and the Corixinae is easily traced via the Cymatiaini. As POISSON & JACZEWSKI (1928) correctly pointed out, the shape of the palar claw and the structure of the apparatus for connecting the hemelytra with the hind wing (the coupling apparatus) resemble those of *Cymatia* FLOR 1860, and it seems plausible that the genus *Stenocorixa* HORVÁTH 1926 is more closely related to *Cymatia* than to any other corixine genus. It is also noteworthy that the Stenocorixinae are the only recent water boatman group possessing the highly flattened and pad-shaped hind tibiae as well as 2-segmented hind tarsi. A similar situation is observed in the Early Cretaceous corixid *Velocorixa ponomarenkoi* YU. POPOV 1986 (Velocorixinae) from the Neocomian of Mongolia (POPOV 1986).

In my opinion HUNGEFORD's (1948) suprageneric classification of the Corixidae, very recently reaffirmed by ŠTYS & JANSSON (1988) without additional evidence, is too formal and hardly corresponds to the family's phylogeny. I believe the recent Corixidae form a well-defined family quite nicely isolated from the related water bug families. It merits separation into four recent subfamilies: Corixinae, Diaprepocorinae, Micronectinae and Stenocorixinae. Each of the latter represents its own conspicuous adaptive lineage, with the Diaprepocorinae being more plesiomorphic (= primitive) as compared to the others. Besides, the Diaprepocorinae share some important characters with terrestrial bug groups.

Fig. 7–10. *Diacorixa germanica* n. sp.
7: Holotype, imago, Inv.-Nr. 26498 (x 13,5), in alcohol, Randeck Maar, Southwest Germany.
8: Holotype, imago, Inv.-Nr. 26498 (x 13,5), Randeck Maar, Southwest Germany.
9: Paratype, imago, Inv.-Nr. 26501 (x 13,5), in alcohol, Randeck Maar, Southwest Germany.
10: Paratype, imago, Inv.-Nr. 1966 XLII 15, in alcohol, Wemding, Southern Germany.

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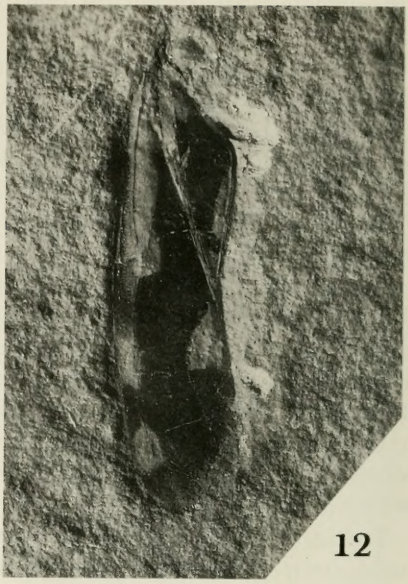

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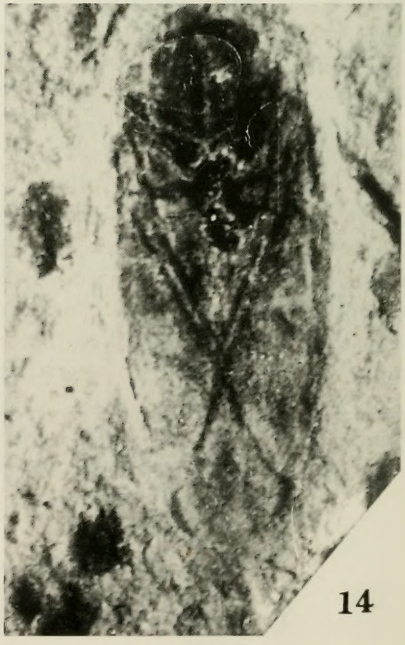

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The subfamily Corixinae in its turn warrants subdivision into two tribes only, Cymatiaini and Corixini. In this respect I support WALTON's (1940, 1943) opinion, whereas HUNGERFORD's (1948) subfamily Heterocorixinae and tribes Agraptocorixini, Glaenocorisini and Graptocorixini are to be merged within the single tribe Corixini. Since the proposal of my earlier (POPOV 1971) subfamilial classification of the Corixidae, with no formal tribes recognized, I am bound to change now my ideas only as regards the status of the Stenocorixinae. This group is indeed very aberrant and conspicuous, particularly concerning the hemelytral morphology, very feeble abdominal asymmetry in the males and absence of strigil, pad-shaped hind tarsi, thereby deserving a subfamilial rather than a tribal rank.

As regards the phylogeny of the Corixoidea as a whole, as well as the interrelationships of the component corixid subfamilies, this problem can hardly be considered as being ultimately solved. The idea of an independent origin of the Corixidae belongs to PARSONS (1965), as opposed to the commonplace opinion about the infraorder Nepomorpha as a monophyletic group. POPOV (1971) and ŠTYS & JANSSON (1988) have postulated the origin of the Corixoidea to have been different from that of the remaining nepomorphan superfamilies. Indeed, the Corixidae in some respects are closer to terrestrial bugs. They, too, have the well-developed and functionable scent glands in both nymphs and imagines, the primitive boatman genus *Diaprepocoris* KIRKALDY 1897 from Australia and New Zealand possesses ocelli on the vertex, etc. Besides, the Corixidae differ from most of the other families of the Heteroptera in having a conspicuous structure of the abdominal apex, being perhaps closer in this respect to the Ochteridae. This idea has been reflected in my phylogenetic schemes of the Nepomorpha (POPOV 1971, 1980, 1981).

My present opinion about the phylogenetic interrelationships of both fossil and recent subfamilies of the Corixidae differs considerably from my older one (POPOV 1986) as shown in Fig. 6.

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Fig. 11. *Diacorixa germanica* n. sp., Paratype, nympha, Inv.-Nr. 26499 (x 16,5), in alcohol, Randeck Maar, Southwest Germany.

Fig. 12. *Diapherinus ornatipennis* YU. POPOV, holotype, hemelytra, PIN no. 1989/3438 (x 6), Baissa, Transbaikalia, USSR.

Fig. 13. *Diacorixa miocaenica* YU. POPOV, imago, holotype PIN no. 372/16 (x 11,5), Tchon-Tuz, North Kirghizia, USSR.

Fig. 14. *Diacorixa miocaenica* YU. POPOV, holotype, PIN no. 372/16 (x 13), in alcohol, Tchon-Tuz, North Kirghizia, USSR.

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